

THE NORTH-EAST ARCTIC COD STOCK'S CONSUMPTION OF VARIOUS PREY SPECIES 1984-1989

by

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ABSTRACT

The North-East Arctic cod stock's consumption of different prey species has earlier been calculated by Mehl (1989) for the period 1984-1986. However, a new model to describe gastric evacuation in cod has now been presented by dos Santos (1990). This model is based on extensive feeding experiments with relevant prey items, done at relevant temperature conditions. This model is combined with the stomach content data to give consumption estimates for each of the years 1984-1989. The results are compared and judged against data on individual cod growth, daily rations and food conversion efficiency.

INTRODUCTION.

One essential requirement for multispecies models is estimates of the food consumption by the main predator stocks over the area of distribution. In addition to data on the number and distribution of the different predator age groups, good estimates of the annual food requirements are needed. The latter can be estimated in two ways:

- from quantitative stomach content data and data on gastric evacuation rates (models)
- from consideration of energy requirements and data on diet composition

The first method has been chosen in several investigations, may be because it consists of more or less straight forward measurements. But these measurements which results in the consumption rates by/of the actual predator/prey stocks are important and sometimes also weak points in the models they are used in.

This is the situation for the MSVPA models both in the North Sea and in the Baltic, and it has the same importance for the multispecies modeling work in the Barents Sea. The first results of this work were presented in Bogstad and Tjelmeland (1990, 1991). In the Barents Sea stomach data were previously combined with temperature-correlated evacuation rates from the North Sea to calculate the cod's consumption rates (Mehl, 1989). Later a preliminary evacuation rate model based on feeding experiments done in Balsfjord, Northern Norway by Jorge dos Santos have been used (Mehl, 1989); (Mehl and Sunnanå, 1991). This evacuation rate model was compared to five other evacuation rate models in Bogstad and Mehl (1990), and the results were then compared with prey stock sizes and data from other investigations on daily ration and food conversion efficiency. The new evacuation rate model given by dos Santos (1990), which is based on experiments done at relevant temperature and with relevant prey, will be used for the consumption calculations made in this paper. The model takes into account both the temperature and the meal size/ body weight ratio in addition to the prey species. As we do not know the meal size from the stomach data, we will need a relationship between the meal size and the stomach content. We will suggest such a relationship, and compare the results with data from other investigations on daily ration and food conversion efficiency as was done in Bogstad and Mehl (1990).

MATERIAL AND METHODS.

The evacuation rate model.

According to dos Santos (1990) the evacuation of a single meal for cod can be described in the following way for prey category i:

$$S_{it} = S_{i0} e^{-\left(\frac{t}{H_i e^{-cT} \left(\frac{S_{i0}}{W}\right)^b}\right)^{K_i} \ln 2}$$

, where S_{it} is the stomach content at time t (hours), S_{i0} is the initial meal size, W the fish body weight and H_i is the evacuation rate constant which is a theoretical value expressing for a given prey i the half-life(hours) of a meal of the same size as the fish body weight at 0°C . T is the temperature in $^\circ \text{C}$, b and c are constants. The shape parameter K_i determines the shape of the evacuation curve. We have here used a notation which differs slightly from the one used by dos Santos (1992).

For consumption calculation purposes, we assume a steady state, i.e. that the amount of food eaten is equal to the amount digested. This means that the ration of prey item i eaten per hour, R_i , becomes

$$R_i = \frac{\ln 2 \cdot S_i \cdot K_i}{H_i \cdot e^{-cT} \cdot \left(\frac{S_{i0}}{W}\right)^b} \cdot \left(\frac{t}{H_i \cdot e^{-cT} \cdot \left(\frac{S_{i0}}{W}\right)^b}\right)^{K_i-1}$$

In dos Santos (1990) it is shown that the shape parameter K_i is not a main contributor to the goodness-of-fit of this single-meal model. He has estimated the parameters both when K_i is allowed to vary and when K_i is restricted to 1.0 for all prey. For all prey except shrimp, the 95% confidence interval for K_i was found to contain the value 1.0 (exponential evacuation) when the model was applied in terms of wet matter of prey. Thus, we have chosen to use the parameter values obtained when K_i is restricted to 1.0 for all prey because this is a more convenient formula to work with. Equation (2) can then be simplified to :

$$R_i = \frac{\ln 2 \cdot S_i \cdot e^{cT}}{H_i \cdot \left(\frac{S_{i0}}{W}\right)^b}$$

The parameter values are (wet weight): $b=0.54$, $c=0.11$, $H=205$ (krill), 533 (shrimp), 452 (herring) and 283 (capelin).

For sequential meals, the best fit was found when the term $\frac{S_{i0}}{W}$ was changed following each new meal, assuming that the 'new' total stomach content is the stimulus driving evacuation. Thus, we will relate the initial meal size S_{i0} to the observed stomach content. We will start by assuming that the initial meal size is equal to twice the observed total average stomach content $S=\Sigma S_i$. The final formula for R_i then becomes:

$$R_i = \frac{\ln 2 \cdot S_i \cdot e^{cT}}{H_i \cdot \left(\frac{2S}{W}\right)^b}$$

The cod stock's consumption in tonnes of prey species i , prey size group j in season l ($C_{i,j,l}$) is then given by

$$C_{i,j,l} = \sum_{k,n} R_{i,j,k,l,n} \cdot XN_{n,l} \cdot XP_{k,l,n} \cdot \text{const}$$

where $R_{i,j,k,l,n}$ is the ration of prey species i , prey size group j in area k and season l for cod age group n , $XN_{n,l}$ is the number of individuals of predator age group n in season l and $XP_{k,l,n}$ is the proportion of individuals of predator age group n in area k and season l . Const is a scaling factor in order to get the consumption in tonnes per season.

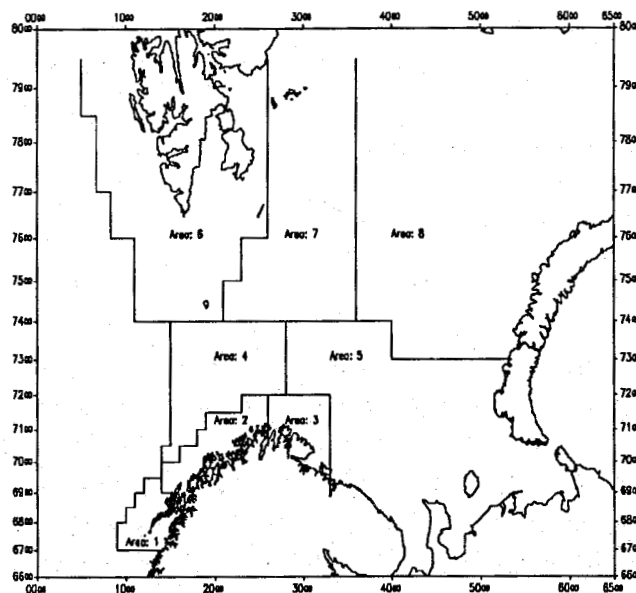
It was decided to apply the evacuation rate for capelin also for amphipods. For cod, haddock and redfish the evacuation rate for herring was applied. For "other" prey species, the evacuation rate for krill was applied for cod age group 1 and 2, because for these age groups "other" consists mainly of smaller crustaceans and other easily digestible food. For the older cod age groups, the evacuation rate for herring was applied, because "other" for these age groups mainly consists of fish prey.

Data used.

The temperatures used are calculated by a temperature model which is also used by the multispecies model for the Barents Sea (MULTSPEC) (Bogstad and Tjelmeland, 1990, 1991). Data from standard hydrographical sections (Fugløya-Bjørnøya, Vardø N, Kola section) are used. At different depths and over different parts of the sections Fourier analysis is used on the temperature data. The temperature is then integrated in time for a representative location in each area to give one temperature for each year, area and month. The procedure is documented in Alvarez and Tjelmeland (1989). A depth of 100m has been used for these calculations. Due to problems with the temperature data base, the temperatures in 1988 have been set equal to the temperatures at the same position/time as in 1987 +0.3 °C, and the temperatures in 1989 have been set equal to the temperatures at the same position/time as in 1987 +0.9 °C. These differences of 0.3 °C and 0.9 °C are equal to the differences in the yearly mean at the Kola section between these years (PINRO, Murmansk, pers.comm.).

Stomach data for the years 1984–1989, collected by IMR and PINRO have been used in the calculations. Details about stomach sampling, analysis and aggregation of data are given in Mehl (1986, 1989) and Mehl and Yaragina (1991). The area distribution used in the multispecies model for the Barents Sea until 1990, which also is the basis for the division of the Barents Sea in areas for consumption calculation purposes, is shown on the map below.

Figure 1 Multispecies area division of the Barents Sea.



The consumption is calculated by 3 areas (II + IV, III + V and VI + VII) for each halfyear and predator age group. Because area VI+VII is sampled only once a year, the data

collected during the second half of the year are also used for the first half of the year. The data collected in 1984 were also used for the first part of 1984. During the second half of 1985 the sampling in the southern part of the Barents Sea (areas II+IV and III+V) was rather poor. Because of the large seasonal changes in the diet in these areas (Mehl, 1986), the data collected for the second part of 1984 in the same areas were used. But the content of shrimp was reduced to the same level (by percentage) as in area VI + VII during the second part of 1985, because of the all-over reduction of the shrimp stock from 1984 to 1985 (Tveranger and Øynes, 1985). In the second half of 1986, data for areas II+IV and III+V combined were used to give the diet for area II + IV due to poor sampling in area II + IV.

Table 5 in the appendix presents the mean weight of cod in 1984–1989 in the first and second half of the year. The weights are calculated using the weight in stock used by the ICES Arctic Fisheries Working group (Anon., 1991a) for ages 3 and older and the average of Norwegian and Russian survey weights for ages 1 and 2 (all at January 1), and assuming that the growth in weight is the same in every quarter during the year. (For the 7–9 group, the weight is calculated as a weighted average of the weights of age groups 7–9). For some of these years, there is a large discrepancy between the Norwegian and Russian survey weights, and this should be kept in mind when evaluating the calculations of daily ration in % of body weight and food conversion efficiency. This discrepancy may to a large extent be due to differences in age reading, and this matter is now under investigation (Anon., 1993). The Working Group makes an arithmetic average of the weight at age from these two surveys.

VPA-data from the Arctic Fisheries Working Group (Anon., 1991a) are used when the total cod stock's consumption is estimated. The number in each age group in the stock in each season is set to be the number in the middle of the season. This is found by reducing the number at the beginning of the year, using one fourth of the yearly natural and fishing mortality for each quarter. For age groups 1 and 2, the number at the beginning of each season is found by back-calculating the number at age 3 (Anon., 1991a) using a yearly natural mortality (M) of 0.2. The numbers are presented in table 6 in the appendix.

The geographical and seasonal distribution of the different cod agegroups are based on survey data, both acoustic and bottom trawl data (Dalen et.al. (1984), Hylen et. al. (1985), Hylen et. al. (1986), Godø et. al. (1987), Hylen et. al. (1988a), Hylen et. al. (1988b), Hylen et. al. (1989), Jakobsen et. al. (1989), Godø et. al. (1989) and unpublished survey data). They are presented in table 7 in the appendix.

DISCUSSION.

The calculated consumption by cod in the period 1984–1989 of the different prey species is shown in table 1.

Table 1 The Northeast Arctic cod stock's consumption in 1000 tonnes of the main prey species in 1984–1989 (% of total consumption in parentheses).

Year Prey species	1984	1985	1986	1987	1988	1989
Amphi- pods	16(1)	113(3)	721(25)	742(35)	1029(44)	646(27)
Shrimp	417(19)	156(5)	125(4)	177(8)	128(5)	137(5)
Capelin	867(40)	1938(56)	956(33)	226(11)	511(22)	783(31)
Herring	66(3)	161(5)	131(4)	30(1)	1(0)	4(0)
Cod	33(2)	47(1)	103(4)	32(2)	10(1)	8(0)
Haddock	45(2)	40(1)	79(3)	3(0)	5(0)	36(2)
Redfish	331(15)	205(6)	251(8)	299(14)	190(8)	213(9)
Others	371(17)	813(23)	565(19)	631(29)	482(20)	670(26)
Total	2146(99)	3475(100)	2932(100)	2141(100)	2355(100)	2497(100)

From the table above, we see that capelin and amphipods were the most important prey species during the period, followed by redfish and shrimp. Young cod (cannibalism), haddock and herring contributed 5% or less each to the total consumption in all years. We see that amphipods, which were almost absent from the diet in 1984 and 1985, were the most important prey in 1987 and 1988. The proportion of capelin in the diet decreased from 1985 to 1987, in accordance with the collapse of the capelin stock, but after that the proportion rose again. The proportion of shrimp in the diet was relatively high in 1984, but stayed at a low level for the rest of the period. Compared to the other prey species, the percentage of redfish and "other" prey in the diet was relatively stable in the period. The cod stock's consumption was highest in 1985, both in tonnes and relative to the biomass of the cod stock at the beginning of the year.

The consumption of redfish, which is relatively stable, is high compared to the biomass of an age group at age 6 (10000–55000 tonnes for *Sebastes mentella* in the period in question, and less for *Sebastes marinus* (Anon., 1991a)). The main part of the redfish consumed is younger than 6 years, and the biomass of an age group of redfish younger than 6 years is less than that at age 6. Thus, the predation by cod on redfish is quite significant.

The decrease in the consumption of shrimp from 1984 to 1985 seem to be consistent with the decrease in the biomass estimate (Tveranger and Øynes, 1985), and the relatively low consumption of shrimp in the following years is also consistent with the biomass estimate time series. The calculated consumption is of the same order as the biomass estimate in the period (Anon., 1991b), which is , however, thought to be an

underestimate. The catch in the period varies between 45 and 120 thousand tonnes, and the predation from cod is thus more important than the catch.

The consumption of mature capelin by cod has been studied by Bogstad and Tjelmeland (1990, 1991). It should be mentioned that for the first half of the year, most of the samples are taken in the first quarter, when there may be intensive predation on mature capelin, and this may lead to an overestimate of the total consumption of capelin.

The high consumption of cod (cannibalism) in the years 1984–1987 may be part of the explanation why the 1984–1986 year classes of cod, which seemed to be very strong at the 0-group stage, turned out to be rather poor. See also Skagen et.al. (1990). To a somewhat lesser extent, this also happened for haddock. The high consumption of haddock in 1989 compared to 1987 and 1988 may be due to an error in the data.

The consumption of herring is highest in the years 1984–1986, coinciding well with the time period when the strong 1983 year class of herring was present in the Barents Sea.

For the age groups 1 and 2, krill and small crustaceans dominate the "other" group. For the older age groups, "other" consists of various crustaceans and small fish. The proportion of fish in "other" increases with age.

Table 2 summarizes the annual consumption per cod for the different age groups:

Table 2 Annual consumption per cod (grams) by age group in the Northeast Arctic cod stock in 1984–1989

Year Age group	1984	1985	1986	1987	1988	1989
1	116	185	72	138	134	143
2	569	681	387	384	455	619
3	1501	1842	1094	879	864	1361
4	2716	3509	2532	1574	1855	2498
5	4823	5660	4785	3120	3452	4105
6	6829	9451	7232	5959	6228	6490
7-9	11307	15996	13583	8811	13430	10641

Table 3 gives the daily consumption per cod in percent of the bodyweight in the middle of the year (daily coefficient).

Table 3 Daily coefficient by agegroup for Northeast Arctic cod in 1984–1989.

Year Age group	1984	1985	1986	1987	1988	1989
1	0.54	0.95	0.42	0.84	0.55	0.48
2	0.56	0.91	0.73	0.82	0.68	0.66
3	0.57	0.78	0.65	0.84	0.68	0.76
4	0.51	0.77	0.63	0.71	0.83	0.82
5	0.54	0.73	0.71	0.60	0.87	0.87
6	0.52	0.76	0.66	0.67	0.81	0.86
7-9	0.59	0.85	0.75	0.53	0.82	0.74

The new evacuation rate model gives a lower consumption estimate than found previously. The introduction of meal size dependence will mostly affect the consumption of capelin, because stomachs with large content usually contains capelin.

We see that the daily coefficient is in the interval 0.4–1.0, which is lower than found in other investigations, see Bogstad and Mehl (1990). Daan (1973) found a drop in the daily coefficient for increasing age for cod in the North Sea. Our calculations do not show such a trend, which leads us to believe that the consumption by the youngest age groups is underestimated. We have relatively few samples of the youngest age groups, and the proportion of empty stomachs is high. Also, in the experiments done by dos Santos cod of sizes corresponding to age 3 and 4 for Barents Sea cod dominated. According to the latest experiments done by dos Santos (pers. comm.) it also seems that the consumption by the youngest fish is somewhat underestimated.

Table 4 presents the annual weight increment in percent of the annual consumption (food conversion efficiency — FCE).

Table 4 Food conversion efficiency (%) by agegroup for Northeast Arctic cod in 1984–1989.

Year Age group	1984	1985	1986	1987	1988	1989
1	55	29	53	32	70	98
2	65	34	34	33	51	46
3	25	26	16	17	41	28
4	19	19	13	13	27	26
5	22	14	11	11	22	21
6	14	9	13	10	17	18

The FCE for the 7–9 age group has not been calculated, because different age groups dominates this group from year to year. Also, the calculations for this group are based on relatively few samples, which leads to a large variation in calculated consumption from year to year.

For the youngest age groups, the FCE is obviously too high. The reason for this is the previously mentioned underestimation of the consumption for these age groups. The consumption estimates seems reasonable compared to the stock estimates of the prey species, while Mehl (1989) found that some prey species were "overconsumed". Still, the predation pressure on some prey year classes is considerable, see e.g. Skagen et. al. (1990).

For cod of medium size, the FCE in 1986/1987 is significantly lower than in the other years. This indicates that the low growth of cod in this period was mostly due to lower energy content in the food (less capelin!), and not so much lower total food consumption. There was, however, low abundance of capelin also in 1988, but a high FCE.

The FCE values above should be compared to values obtained from feeding experiments. Values of FCE obtained for fish in capture can be regarded as an upper limit. It would of course be very interesting to redo these calculations using energy content and not wet weight as done here.

Future improvements: The evacuation rate model could be improved by doing experiments with small and large cod and other prey species (redfish, amphipods, gadoids). Also, more experiments with multiple feeding should be performed. In order to make the best possible use of the new evacuation rate model, new calculations should be done based on individual stomach content and predator size data. It should then also be possible to use the actual temperature at the sampling site. The stomach sampling should be improved in order to get a better coverage in area and time. The differences in predator distribution, stomach content and temperature between bottom and pelagic should also be taken into account by trying to sample more representatively. The stomach content data have so far not been weighted by catch rate, due to data base problems. For the multispecies model in the Barents Sea, it is at the moment most important to get a precise estimate of the consumption of capelin by cod. Given a stock estimate of cod and of capelin, the uncertainty in the consumption estimate should not exceed the uncertainty in the stock size estimates.

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Appendix A Cod stock data used.

Table 5 Cod weight-at-age (kg)

Cod age Year/ season	1	2	3	4	5	6	7-9
1984-I	0.042	0.182	0.625	1.328	2.160	3.225	4.883
1984-II	0.074	0.367	0.815	1.583	2.680	3.855	5.468
1985-I	0.040	0.148	0.578	1.075	1.913	3.163	4.825
1985-II	0.067	0.262	0.813	1.405	2.318	3.608	5.415
1986-I	0.036	0.113	0.365	1.010	1.708	2.755	4.613
1986-II	0.055	0.178	0.455	1.170	1.983	3.225	5.238
1987-I	0.034	0.096	0.248	0.550	1.330	2.265	4.273
1987-II	0.056	0.159	0.323	0.650	1.498	2.555	4.718
1988-I	0.043	0.125	0.270	0.485	0.893	1.840	3.575
1988-II	0.090	0.242	0.430	0.735	1.278	2.360	4.565
1989-I	0.047	0.186	0.395	0.673	1.075	1.768	3.490
1989-II	0.117	0.328	0.585	0.998	1.505	2.363	4.370

Table 6 Number of individuals (million) of each age group by season and year.

Cod age Year/ season	1	2	3	4	5	6	7-9
1984-I	1121	572	363	125	73	42	34
1984-II	1014	517	326	107	57	29	17
1985-I	334	917	463	282	85	41	23
1985-II	302	830	410	237	64	28	13
1986-I	250	273	747	352	184	44	24
1986-II	226	247	668	292	131	27	13
1987-I	256	205	222	573	222	83	22
1987-II	231	185	198	471	155	47	12
1988-I	209	209	166	173	362	104	32
1988-II	190	190	149	146	260	67	17
1989-I	261	171	170	129	120	184	52
1989-II	236	155	152	107	96	128	33

Table 7 Proportion of individuals by age group, area, season and year for the Northeast Arctic cod stock in 1984-1989

Area	Year- Season	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6	Age 7-9
II+IV	1984-1	0.002	0.109	0.322	0.417	0.573	0.576	0.782
III+V	1984-1	0.980	0.827	0.653	0.544	0.398	0.409	0.208
VI+VII	1984-1	0.018	0.064	0.025	0.039	0.029	0.015	0.010
II+IV	1984-2	0.002	0.109	0.322	0.417	0.490	0.393	0.540
III+V	1984-2	0.980	0.827	0.653	0.544	0.453	0.577	0.439
VI+VII	1984-2	0.018	0.064	0.025	0.039	0.057	0.030	0.021
II+IV	1985-1	0.000	0.000	0.057	0.288	0.664	0.840	0.923
III+V	1985-1	0.654	0.917	0.854	0.479	0.302	0.058	0.000
VI+VII	1985-1	0.346	0.083	0.087	0.233	0.033	0.102	0.077
II+IV	1985-2	0.000	0.000	0.057	0.288	0.631	0.737	0.847
III+V	1985-2	0.654	0.917	0.854	0.479	0.302	0.058	0.000
VI+VII	1985-2	0.346	0.083	0.087	0.233	0.066	0.204	0.153
II+IV	1986-1	0.000	0.000	0.057	0.332	0.660	0.883	0.848
III+V	1986-1	0.991	0.868	0.846	0.550	0.295	0.066	0.000
VI+VII	1986-1	0.009	0.132	0.096	0.119	0.045	0.050	0.152
II+IV	1986-2	0.000	0.000	0.057	0.332	0.615	0.833	0.600
III+V	1986-2	0.991	0.868	0.846	0.550	0.295	0.066	0.000

Table 7 (Continued) Proportion of individuals by age group, area, season and year for the Northeast Arctic cod stock in 1984-1989

VI+VII	1986-2	0.009	0.132	0.096	0.119	0.090	0.100	0.400
II+IV	1987-1	0.000	0.110	0.220	0.592	0.830	0.712	0.800
III+V	1987-1	0.333	0.292	0.206	0.298	0.080	0.086	0.000
VI+VII	1987-1	0.666	0.599	0.574	0.110	0.090	0.203	0.200
II+IV	1987-2	0.000	0.090	0.060	0.282	0.464	0.394	0.600
III+V	1987-2	0.133	0.242	0.054	0.140	0.044	0.048	0.000
VI+VII	1987-2	0.867	0.667	0.887	0.578	0.492	0.559	0.400
II+IV	1988-1	0.000	0.000	0.307	0.480	0.514	0.477	0.500
III+V	1988-1	1.000	0.590	0.475	0.275	0.268	0.114	0.000
VI+VII	1988-1	0.000	0.410	0.218	0.245	0.218	0.409	0.500
II+IV	1988-2	0.000	0.000	0.201	0.234	0.338	0.367	0.600
III+V	1988-2	1.000	0.200	0.311	0.134	0.124	0.088	0.000
VI+VII	1988-2	0.000	0.800	0.488	0.632	0.538	0.545	0.400
II+IV	1989-1	0.222	0.286	0.164	0.286	0.407	0.601	0.639
III+V	1989-1	0.667	0.643	0.639	0.586	0.483	0.324	0.250
VI+VII	1989-1	0.111	0.071	0.197	0.128	0.110	0.075	0.111
II+IV	1989-2	0.222	0.310	0.134	0.046	0.083	0.125	0.115
III+V	1989-2	0.667	0.619	0.669	0.826	0.708	0.725	0.691
VI+VII	1989-2	0.111	0.071	0.197	0.128	0.209	0.150	0.194